Diversity and Vertical Distribution of Lichens in a Venezuelan Tropical Lowland Rain Forest

Harald Komposch* and Josef Hafellner

Institut für Botanik, Holteig. 6, 8010 Graz, Austria. E-mail: harald.komposch@kfunigraz.ac.at

ABSTRACT. As part of Project Surumoni, an investigation was conducted in 1997–1998 on species diversity and vertical distribution of lichenized fungi within a tropical lowland rain forest in southern Venezuela. A tower crane at Surumoni, which gives easy access to all forest strata, facilitated the investigation. In the plot, nine trees were selected as phorophytes on which 250 species of lichenized fungi were observed. Study results showed crustose lichens as the dominant life form. Of these, Thelotremataceae, Graphidaceae, and Trypetheliaceae contributed to nearly three quarters of total species richness. The species spectrum showed a well-defined vertical stratification from forest floor to top of canopy. At ground level, shade-tolerant species (chiefly Thelotremataceae) occurred. Moving upward, the proportion of Graphidaceae and Trypetheliaceae increased continuously, but Thelotremataceae appeared to remain constant up to the inner canopy. Higher yet, Thelotremataceae were less frequent, with Graphidaceae and Trypetheliaceae dominating. The degree of species turnover along the vertical gradient is shown in several diagrams for trees of stratum A and B separately. Species replacement is highest between height zones 1 and 2 for investigated trees of stratum A, but the more uniformly barked trees of stratum B do not show this marked difference. Calculation of additive beta turnover reveals, depending on substratum, three to nearly four complete species turnovers along the vertical gradient in the forest.

Key words: lichenized fungi, tropical rain forest, vertical distribution, alpha and beta diversity, canopy research, Venezuela

Introduction

Tropical rain forests are rich in lichenized fungi, most of which live epiphytically on bark and living leaves. Recent research has covered biodiversity and taxonomical aspects of cryptogams (e.g., Aptroot 1997a; Aptroot et al. 1995, 1997; Gradstein 1995; Lücking 1998a; Lücking & Matzer 1996; Sipman 1992, 1997a; Sipman & Aptroot 1992; Sipman & van Aubel 1992). Few authors, however, have concentrated on ecological questions, and most of their conclusions were based more on suggestions and estimates than on primary data achieved with accuracy. A number of ecological papers have comparatively good information on foliicolous lichens (Lücking 1994, 1995, 1997a, 1998b; Sipman 1997b) and some information on corticolous macrolichens and bryophytes (Cornelissen & ter Steege 1989; Cornelissen & Gradstein 1990; Montfoort & Ek 1990; Wolf 1993a, 1993b). Little data, though, exist on crustose corticolous lichens in lowland rain forests, with the exception of an unpublished master's thesis (Montfoort & Ek 1990). This lack of information may be explained by the poorly known taxonomy of tropical lichens, as well as by the difficulties of canopy access (Sipman & Aptroot 1992). Monographic treatments of tropical lichen taxa are scarce and often based on insufficient collec-

tions. Thus the statement of Rhoades (1995: 368) that "cryptogams of tropical forest canopies are the least well known in the world" remains valid and reflects an incomplete knowledge of tropical corticolous lichens (Aptroot 1997b: 38).

Cornelissen and ter Steege (1989) were the first to describe 13 cryptogamic communities along a vertical gradient within an evergreen wallaba forest in Guyana. They confirmed that the six height zones introduced by Johansson (1974: 116) and by Longman and Jeník (1987: 102) are practicable for cryptogamic work in tropical rain forests. They did not deal in detail, however, with crustose lichens. Later, Montfoort and Ek (1990) visualized the key role of crustose lichens and clearly demonstrated spatial distribution patterns of lichens and bryophytes within a virgin lowland rain forest in Guyana. Sipman and Harris (1989) roughly outlined lichen zonation from base to crown and cited moisture and light conditions as the predominant regulators (see also Gradstein & Pócs 1989: 312, Lücking 1997b: 105, Richards 1984: 1238). The microclimate of a tropical rain forest has main features that apparently change greatly from canopy top to forest floor. Richards (1996: 206) observed a sharp decline in solar radiation and light received below the canopy, with only a small fraction reaching the forest floor. Maxima, means, and ranges of temperature also decrease, but minimum temperatures are similar at all lev-

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* Corresponding author.

els of the forest. Wind speeds decline to near zero within the forest, and daytime relative humidity readings are higher at lower levels than in the upper canopy. For an overview of vertical stratification in microclimate, see Kira and Yoda (1989). In response to the poikilohydric character of lichens, the high number of microclimatic niches within a forest stand support a vast radiation of species. Each species has individual claims to light, moisture, throughfall, temperature, substratum, stemflow, and other environmental factors. Combined with infraspecific as well as interspecific dependencies, these claims lead to distinct anatomical, morphological, and chemical adaptations.

As part of the interdisciplinary Project Surumoni, our study attempts to answer the following questions: How diverse is the lichen flora (alpha species diversity) within this tropical lowland rain forest? Does vertical distribution of species or families reveal patterns? And if so, how can the species turnover along height zones (beta diversity) be characterized?

MATERIALS AND METHODS

Field studies were carried out in February 1997 and 1998. Lichen specimens, air-dried in paper capsules, were sent via the Instituto Botanico of Caracas to Graz. There, they were prepared, labeled, and determined, using a Leica MZ6 Microscope and a Zeiss Axioscope with drawing tube. Photographs were taken with a Minolta X-700, fixed at the original Leica Phototube and illuminated by two flashbulbs. Most chemical tests were made using TLC (White & James 1985). For uncertain identifications or small amounts of lichen material, we used a BIO-TEK KONTRON-HPLC-System to gain further data (Feige et al. 1993). Identified, cited specimens are deposited in the GZU and VEN herbaria. Specimen labels carry tree numbers that correspond to numbers on aluminum tags fixed to each tree in the study plot.

Study Site

The investigation took place in an evergreen lowland rain forest in the upper Orinoco River Basin of Venezuela. The study site was ca. 15 km west-southwest of La Esmeralda on the west bank of Río Surumoni, a small blackwater tributary of the upper Orinoco River at 3°10′23″N, 65°40′27″W, and ca. 105 m elevation. A 40-m tall tower crane with a 40-m jib-boom mounted on 120-m long railways gave easy access to all height zones in the 1.5 ha forest plot.

The climate of the study site is tropical, with a mean annual precipitation of ca. 3000 mm.

Year-to-year fluctuations of 500 mm are common (Anhuf pers. comm.) The December–March period, however, is rather dry with a high possibility of consecutive dry days.

The physiognomy of waterlogged forest, found only in small scattered segments, is a mesophyll-dominated, somewhat open rain forest growing on sandy terra firma soil, where strata A, B, and C are distinguishable (Richards 1996: 34).

Stratum A. With emergent trees absent in the crane plot, stratum A is not very distinct, and trees rarely exceed heights of 30 m. Some individuals of the predominating genera Goupia and Qualea belong to this uppermost layer. Although indigenous inhabitants state that the Surumoni area has not been cleared or logged in historic time, the abundance of Goupia glabra Aubl. indicates a certain disturbance, the causes of which remain obscure (Richards 1996: 461).

Stratum B. With smaller trees up to heights of 20 m, stratum B is characterized by the frequent occurrence of lianas and palms, especially Oenocarpus and Euterpe. The usually small and conically crowned trees stand close together. Along with the intermixed higher trees of stratum A, they form a more or less continuously closed canopy with considerable differences in height levels.

Stratum C. The upper strata did not appear very dense, and sparse shrubs and herbs allowed visitors to walk through stratum C rather easily.

Only Coomes and Grubb (1996) have provided data on similar forest types at La Esmeralda that indicate much greater human disturbance. Detailed reports on the structure and physiognomy of the Surumoni forest within the crane plot await publication. As a result of severe flooding in 1996, the lower trunks of trees standing in the southernmost part of the plot, on the edge of a terra firma terrace, were covered with loam up to ca. 1 m. As most lichens and bryophytes had died or were rubbed off, the trees of this area were excluded from the present study.

Sampling Design

Nine phorophyte trees were selected, seven belonging to stratum A and two to stratum B. Because of ecological differences in architecture and substrate, the two strata were handled separately in terms of vertical distribution. The seven trees of stratum A belong to the two codominant species Goupia glabra (Celastraceae, Nos. 170, 539, 909, 991) and Qualea species (Vochysiaceae, Nos. 178, 209, 313). Trees of stratum A generally have wide, sweeping crowns up to

a diameter of ca. 10 m, with large, inclined branching systems that insert at heights of 13–17 m above ground. The sampled genera *Goupia* and *Qualea* have neither buttresses nor other modified root systems, and their diameter at breast height (dbh) is 70–90 cm. Typical for these phorophytes is a change of bark characteristics with age. Bole bark is slightly fissured to rough; and at the stem base, it is often more weathered and scaling. Upward on the first big branches (height zone 4), the bark becomes stable and smoother. Generally *Qualea* has a smoother and more stable bark, whereas *Goupia* has a strongly flaking bark on the bole, which in the study area is often enhanced by the mining activity of ants or termites. In contrast, the sampled trees of stratum B, *Couma rigida* Müll.Arg. (Apocynaceae, No. 511) and an unidentified tree (No. 947), have small, tapering crowns, with lateral diameters of 4–5 m and straight, slender trunks (<20 cm dbh), seemingly unbranched to the top. Thin twigs appear at heights of 15–19 m. Their stable, relatively smooth, and thin bark surface remains constant over the entire bole (Richards 1996: 75). Phorophyte data refer to a unpublished species list provided by Rainer and Wesenberg.

For sampling purposes, each tree was divided schematically into six height zones (after Cornelissen & ter Steege 1989), designed to correspond to natural zones of environmental conditions (Johansson 1974: 68, Komposch & Nieder unpubl. data). Each tree trunk was divided into three height zones: the trunk base up to 2 m above the ground (height zone 1) and the lower half (height zone 2) and upper half (height zone 3) of the remaining trunk. The forest canopy also was divided into three height zones. The outer canopy (height zone 6) was defined as a thin layer down to 2 m from the tips of the twigs. The lower part of the canopy was divided into two equal halves: the middle (height zone 5) and the inner canopy (height zone 4). Within each height zone, we used a hand lens (10×) and collected specimens of every distinct lichen thallus and bryophyte. For this phase of the investigation, the remote-controlled crane gondola proved a comfortable tool. In cases where the crowns were too dense to penetrate, the single-rope technique was used to sample tree trunks (Perry 1978).

Data Management

Data were stored and handled in a Microsoft Access 97 database. Diagrams were created and data processing performed using Microsoft Excel 97 and Statistica 4.0, respectively. Alpha species-diversity (in the sense of Whittaker

1977) as a measurement of heterogeneity (Peet 1974) was expressed by the Shannon index:

$$H' = -\sum_{i=1}^{n} p_i \times \log_{10}(p_i)$$

In the index, n is the number of species, and p_i a relative importance value calculated by the formula:

$$p_i = \frac{n_i}{N}$$

In the formula, n_i is the absolute importance value counting the frequency of lichens, and N is the total sum of the importance values of all species in the plot (Shannon 1949). Species similarities QS between different height zones within trees were computed according to Sørensen (1948) using the formula:

$$QS = \frac{2 \times n_{a=b}}{n_a + n_b} \times 100$$

In the Sørensen formula, n_a is the number of species at the first step, n_b is the number of species at the next step, and $n_{a=b}$ is the number of species shared by both steps. Internal beta diversity is further expressed by the species turnover along the environmental gradient within the forest calculated after Wilson and Shmida (1984):

$$\beta_T = \left| \frac{g_H + l_H}{2 + \bar{\alpha}} \right|$$

This measure of beta turnover β_T combines the idea of species turnover reflected by the gain g and loss l of species along the gradient H, with a standardization by average sample richness $\bar{\alpha}$. The advantages of this method are the independence from internal alpha diversity (Whittaker 1977: 5), sample size, and the partial additivity. The latter allows for an estimation of the degree of community turnover within the whole system. A strict additivity cannot be ensured because alpha diversity of the end samples (height zones 1 and 6), at least in part, vary considerably from the average alpha diversity of all height zones.

RESULTS AND DISCUSSION

Species Richness

A total of 2293 corticolous lichen specimens were collected. About 261 were sterile thalli that often could not be classified to family level. Another 202 specimens in poor condition were omitted from the analyses. The remaining 1830 specimens represented 250 species, of which 14 species were uncertain determinations. Another 142 specimens were recognized but could not be

TABLE 1. Families of lichenized fungi ordered by their total number of species, Surumoni Project, Venezuela, 1997–1998.

Families	No. species
Thelotremataceae	69
Graphidaceae	62
Trypetheliaceae	39
Bacidiaceae	15
Arthoniaceae	10
Roccellaceae	9
Coccocarpiaceae	7
Trichotheliaceae	5
Pyrenulaceae	5
Parmeliaceae	4
Gomphillaceae	4
Opegraphaceae	3
Ectolechiaceae	2
Arthopyreniaceae	2
Gyalectaceae	2
Lecanoraceae	2
Pilocarpaceae	2
Crocyniaceae	1
Meruliaceae	1
incertis sedis	1
Melaspileaceae	1
Verrucariaceae	1
Physciaceae	1
Solorinellaceae	1
Lecideaceae s.l.	1
Total	250

assigned to described species. They were labeled species 1 through species n. Missing numbers among the unknown species mentioned in this article represent specimens collected from trees outside the study's nine-tree subset. These undetermined specimens need further treatment, as several are expected to become newly described species. The corresponding primary data matrix is published in Komposch and Hafellner (1999).

The frequency of collected species reveals a small important group (15%) found regularly (8–27 times); 46% occur less frequently (2–7 times); and a large alliance (39%) was sampled just once.

Although diversity indices are not in common use in lichenological literature, internal alpha diversity is expressed here as a value for future comparison: $H' = -2.19$. The 250 species of lichenized fungi represent the 25 families listed in TABLE 1. Within the study area, the three crustose families (Thelotremataceae, Graphidaceae, and Trypetheliaceae) constitute ca. 70% of total species richness. Minor changes may be expected when critical genera are studied further in such families as Bacidiaceae, Arthoniaceae, and Trypetheliaceae.

In contrast, a study conducted near Saül in Guyana (Montfoort & Ek 1990) revealed a more even distribution of corticolous lichen species among a markedly higher number of 33 families. Although Graphidaceae, Thelotremataceae, and Trypetheliaceae also are dominant near Saül, they contribute just 43% of overall species richness. Furthermore, some of these families are reported to have maximum diversity at higher elevations than in lowland areas. Such families include Pannariaceae, Megalosporaceae, Collemataceae, and Stictaceae (Sipman & Harris 1989: 304).

In general, the forest at Surumoni is extraordinarily diverse in lichen flora, especially in crustose lichens, with vascular epiphytes and bryophytes being comparatively rare. To date, the 250 lichen species detected on nine trees within a 1.5 ha plot are the highest reported for a lowland rain forest, thus contrasting with the assumption by Sipman (1989: 474) that lichen flora is generally poor at low elevations. Near Saül, for example, Montfoort and Ek (1990) had to observe 28 phorophytes to discover 209 species of lichenized fungi (foliicolous lichens included). In the Surumoni study, this figure was attained after observing only eight trees and excluding foliicolous taxa (FIGURE 1). Furthermore, the absolute numbers of species per tree were clearly higher at Surumoni (minimum 45 spp., average 65 spp., maximum 84 spp.) than in Guyana (12, 33, 55). In addition, the rapid ascending cumulative species area curve at Surumoni contrasts with the results of Wolf (1993c: 931). Our data indicate a markedly higher total species richness, particularly when additional substrata (e.g., other tree species, palms, shrubs, and leaves) are included. Thus an alteration of the cautious diversity estimate by Aptroot and Sipmans (1997: 101) is appropriate. Instead of more than 300 species per km², the assumed total species number for tropical lowland rain forests may well exceed 300 species per hectare. The life form diversity among lichens in the nine-tree subset at Surumoni will be discussed in a future publication.

Vertical Distribution

For lichens growing on trees of stratum A, the species spectrum shows a well-defined vertical stratification from forest floor to canopy top. No lichen species found more than two times grows exclusively in one height zone, with the exception of those regarded as pioneers in the outer canopy and perhaps some growing in height zone 1. In the following species arrangement within the six height zones, referenced names are frequently observed, typical, or conspicuous species of lichenized fungi.
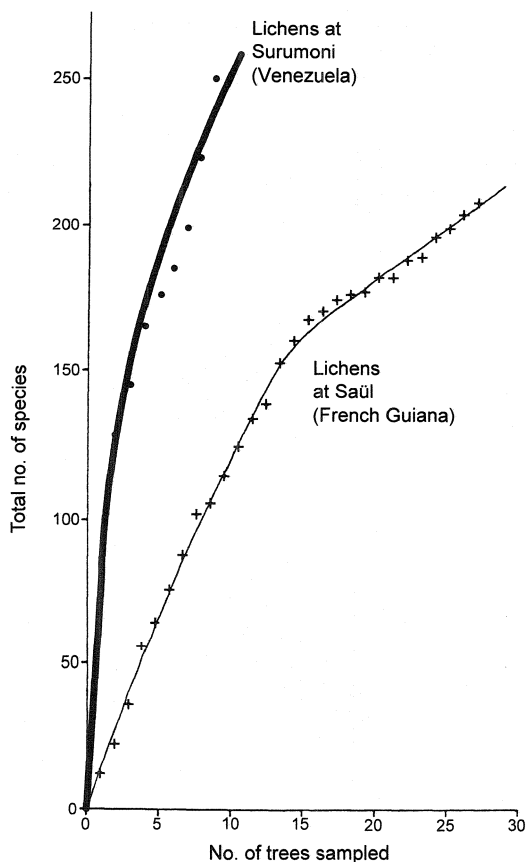
FIGURE 1. Species area curve comparing two rain forest sites, one at Surumoni (Venezuela) with one at Saül (French Guiana). Figure adapted from Montfoort and Ek (1990).

Height zone 1. Starting at the ground level in height zone 1 (tree base), the shade-tolerant lichens that occur include *Lecidea granifera* (Ach.) Vain., *Chroodiscus* sp. 7, *Eschatogonia prolifera* (Mont.) R.Sant., *Ocellularia landronii* Hale, *Thelotrema brasiliana* Hale, one unidentified *Eschatogonia* sp. (FIGURE 2), and a sorediate undescribed species of *Myeloconis*. Lichen vegetation is scanty, with patches of tree trunk lichen-free. According to Sipman and Harris (1989: 304), the shade and permanent moist trunk bases of a tropical rain forest should be dominated by bryophytes in competition with lichens, with species such as *Coenogonium, Leptogium,* and *Porina.* Just one sterile specimen of *Coenogonium* and no specimens of *Leptogium* or *Porina* were collected at the Surumoni study site, and no disturbance indicator species were found in the lower height zones. The absence of such species as *Bulbothrix goebelii* (Zenker) Hale, *Gassicurtia coccinea* Fée, *Myriotrema ter-*

ebratulum (Nyl.) Hale, and *Trypethelium aeneum* (Eschw.) Zahlbr. supports the theory that the forest is at least not heavily disturbed. The scarcity of bryophytes indicates that, in this particular rain forest type, lower trunks and bases of larger, rough-barked trees are not favorable substrata for lichens and bryophytes. Richards (1996: 150) stated that "The trunks of larger trees are seldom completely covered with a continuous carpet of bryophytes." In height zone 1, observations on additional trees, especially understory trees, that host an abundant lichen flora strongly support inappropriate substratal conditions (i.e., strongly weathered and flaking bark) rather than the extreme climatic environment suggested by Richards (1984: 1252). Nevertheless, the description of the higher zones by Sipman and Harris (1989: 304) agrees with the present investigation.

Height zone 2. The lower trunk leads upward through height zone 2 with distinct changes in species composition. *Byssoloma leucoblepharum* (Nyl.) Vain., *Ocellularia exigua* Müll.Arg., and *O. lepadinoides* (Leight.) Zahlbr. are found from the trunk base to the middle of the trunk. Although *Myeloconis parva* P.M.McCarthy & Elix, *O. comparabilis* (Kremp.) Müll.Arg., and *O. auberiana* (Mont.) Hale are found here exclusively (each recorded once in the nine-tree subset), they also grow in neighboring height zones on other trees in the plot. *Erythrodecton granulatum* (Mont.) G.Thor (FIGURE 2), *Phaeographis* sp. 6, *Myriotrema glaucophaenum* (Kremp.) Hale, *O. astrolucens* Sipman, and several unidentifiable *Ocellularia* species are equally distributed among the lower and the upper trunk. Concerning *O. comparabilis* and *M. glaucophaenum,* Hale (1974: 17, 1978: 23) stated that the species occur on lower trunks in rain forests. The hitherto known habitat of *O. astrolucens* was tree trunks in a stunted forest in oligotrophic conditions (Sipman & Aptroot 1992: 97).

Height zone 3. Several species prefer the environment of height zone 3 (upper trunk), namely *Graphina confluens* (Fée) Müll.Arg., *G. incrustans* (Fée) Müll.Arg., *Graphina* sp. 17, *Phaeographina caesiopruinosa* (Fée) Müll.Arg., *Ocellularia sorediata* Hale (described by Hale 1974: 27 on the mid-bole of a rain forest tree in Dominica), *O.* cf. *megalostoma* Müll.Arg., *Pyrenula minor* Fée, *Enterographa* sp. 5, *Chiodecton sphaerale* Ach., and *Chiodecton* cf. *sphaerale.* Although not specific to zone 3, many of these species are best represented there. *Myriotrema neofrondosum* Sipman, a schizidiate crust, provides a good example of the value of canopy research. Described as usually sterile
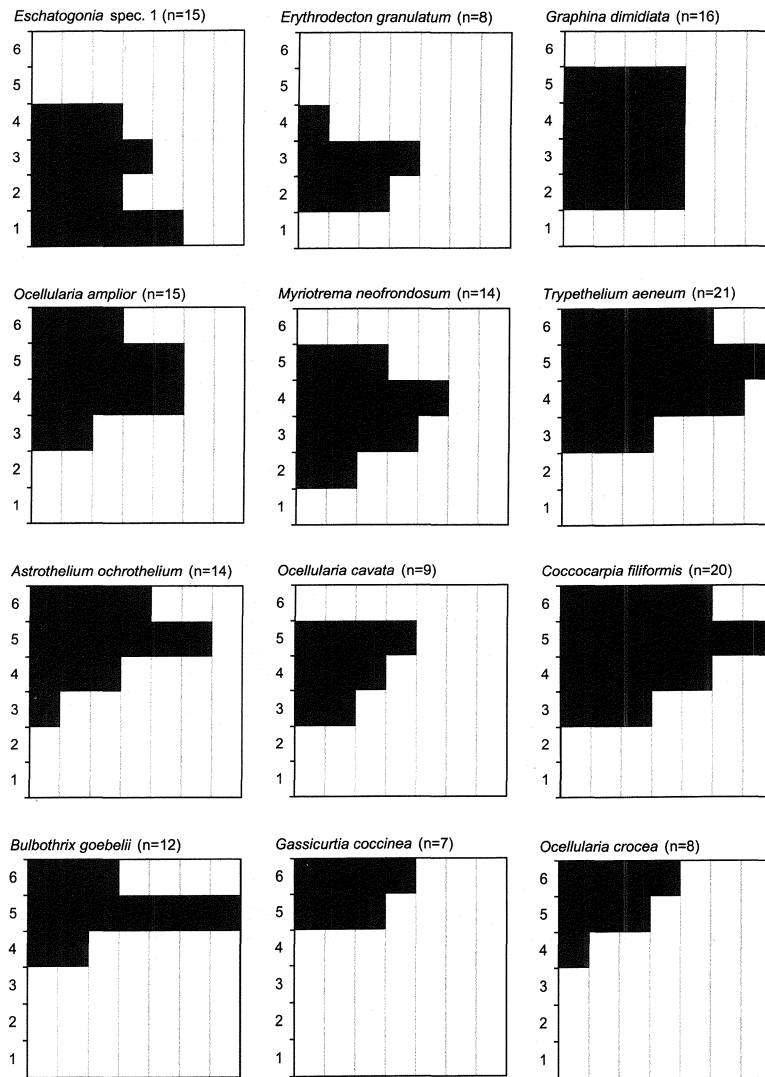
FIGURE 2. Stratum A vertical distribution of selected lichens on phorophytes (*Goupia glabra* and *Qualea* sp., altogether seven tree individuals) at Surumoni; x-axis = number of tree individuals on which a lichen species was observed; y-axis = height zones in which a lichen species was observed.

(Sipman & Aptroot 1992: 85), this species, which is almost always sterile in height zone 2, displays abundant fruitbodies from the upper trunk to the middle canopy. As tree bark becomes more stable and light conditions enhance, the total lichen cover increases to nearly 100%. A few Trypetheliaceae intermingle between thalli of the undescribed *Opegrapha* sp. 1, *Chroodiscus* sp. 9, *Phaeographina* sp. 1, *Graphis* sp. 9, *Sarcographa labyrinthica* (Ach.) Müll.Arg., *Porina farinosa* Knight, *Pyrenula* cf. *brunnea* Fée, and specimens belonging to such genera as *Ocellularia* and *Enterographa*.

Height zone 4. The inner canopy (height zone 4) is dominated by representatives of the Graphidales, especially *Graphis grammitis* Fée, *G. illinata* Eschw., *G.* cf. *dumastii* (Fée) Spreng., *Graphinia insculpta* (Eschw.) Müll.Arg., *G. dimidiata* (Vain.) Zahlbr. (FIGURE 2), *G. interstes* Müll.Arg., *Ocellularia amplior* (Nyl.) Redinger (FIGURE 2), *Myriotrema neofrondosum* (FIGURE 2). Other species include *Arthonia meissneri* Müll.Arg., *A. complanata* agg. Fée, *Enterographa* sp. 1, and the frequent but inconspicuous foliose cyanolichens *Coccocarpia erythroxyli* (Spreng.) Swinscow & Krog, *C. imbricascens*

Nyl., and *C. domingensis* Vain. A large number of lichens found in height zone 4 only once include *Polymeridium albidum* (Müll.Arg.) R.C.Harris, *Astrothelium* sp. 5, *Trypethelium* sp. 3, *Macentina* sp. 1, *Myriotrema myrioporum* (Tuck.) Hale, *M. norsticticum* (Hale) Hale, and many Graphidaceae and other Thelotremataceae. Montfoort and Ek (1990: 31) reported that the upper sides of horizontal branches were covered with a continuous layer of humus and debris on which a closed mat of bryophytes and vascular epiphytes was found. Crustose lichens were restricted mainly to the lateral sides of branches. At Surumoni, where humus layers were de facto absent, conditions for bryophytes were less favorable, and lichens dominated even the upper sides of horizontal branches.

Height zone 5. Moving outwards to the big branches of height zone 5 (middle canopy), a remarkable shift in species composition was observed. *Trypethelium aeneum* was the most noticeable species in the large alliance of Trypetheliaceae that dominated this height zone in species richness as well as in coverage (FIGURE 2). Among them can be found the gray-green *T. nitidiusculum* (Nyl.) R.C.Harris, the bright orange pointed *Astrothelium galbineum* Kremp., *A. ochrothelium* (Nyl.) Müll.Arg. (FIGURE 2), *A. versicolor* Müll.Arg., and less conspicuous species such as *A. subfuscum* Kremp., *T. ochroleucum* (Eschw.) Nyl., *Pseudopyrenula subnudata* Müll.Arg., *Polymeridium quinqueseptatum* (Nyl.) R.C.Harris, and *P. catapastum* (Nyl.) R.C.Harris. Frequent within the whole but most frequent in the middle canopy were *Myriotrema terebratulum* and *Ocellularia cavata* (Ach.) Müll.Arg. (FIGURE 2), both previously reported as canopy species (Hale 1974: 17, 28, 1978: 33), together with *Graphina abaphoides* (Nyl.) Müll.Arg., *Graphina* sp. 7, *Phaeographis* sp. 3, *Melanotheca* sp. 1, and others. In contrast, *Cresponea proximata* (Nyl.) Egea & Torrente, *O. berkeleyana* (Mont.) Zahlbr., *G.* cf. *hologlauca* (Nyl.) Zahlbr., and many unidentified thalli were collected in height zone 5 just once. As an exception, large foliose *Parmotrema* thalli relieved the monotony of the dominating crustose lichens. *Parmotrema* cf. *dilatatum* (Vain.) Hale, *P. margaritatum* (Hue) Hale, and *Parmotrema* sp. 1 were the identified species. The small, foliose, and adpressed thalli of *Coccocarpia filiformis* Arv. (FIGURE 2), *C. stellata* Tuck., and *Bulbothrix goebelii* (FIGURE 2) often grew over bryophytes and other crustose lichens. A genus observed only in the middle and outer canopy was *Gyalideopsis,* with *G.* cf. *palmata* Kalb & Vezda, *G. lambinonii* Vezda, and two unidentifiable species, all inconspicuous lichens. Despite

careful observations, some species were overlooked in the field but incidentally detected under the microscope. Such was the case repeatedly with *Myriotrema minutulum* (Hale) Hale and *Graphis* sp. 11.

Height zone 6. Lichens that settled first on the thin branches of height zone 6 (outer canopy) usually had small, light-colored or white thalli and very small, often carbonized or dark-colored fruitbodies (Lücking 1997b: 106). On the one hand, juvenile thalli were observed of species that occurred in height zone 5, such as *Trypethelium nitidiusculum, Gassicurtia coccinea* (FIGURE 2), *Graphis afzelii* Ach., *Astrothelium galbineum, Celothelium dominicanum* (Vain.) M.B.Aguirre, *Pseudopyrenula diluta* (Fée) Müll.Arg., *Polymeridium subcinereum* (Nyl.) R.C.Harris, *P. pleurothecium* R.C.Harris, *Ocellularia crocea* (Kremp.) Overeem & D.Overeem (FIGURE 2), *Graphina malmei* Redinger, and *Graphis* sp. 8. On the other hand, some seemed to be strictly restricted to this extreme outpost, for example *Polymeridium albocinereum* (Kremp.) R.C.Harris, the only identifiable one in the following alliance: *Chroodiscus* spp. 10, 11, and 12, *Graphis* spp. 3, 7, and 14, *Phaeographis* spp. 5 and 7, and *Graphina* sp. 12.

The total number of lichen species per height zone for trees of stratum A is shown in TABLE 2. From trunk base to middle canopy, the species numbers continuously increase from 20 to 99, then decline to 63 in the upper canopy. In contrast, Montfoort and Ek (1990: 21) found the highest values in the upper canopy, with lichen cover showing a second minimum at height zone 5. The difference in species numbers between Surumoni and Saül may be attributed to different site conditions in Venezuela and French Guiana (Montfoort & Ek 1990: 31). Field observations suggest that competition of bryophytes does not play a major role at Surumoni. Another factor may be the alteration of the borderline between height zones 5 and 6, which causes a shift of species to zone 5. Although comparisons of species numbers in different height zones that vary that much in surface area are not meaningful. Interesting conclusions concerning the biodiversity of a forest stand, however, can be drawn by projecting the tree base species numbers to the whole tree. Considering bark characteristics for trees of stratum A, we calculated roughly the total species richness of a single tree as 23 times greater than that of height zone 1. For smooth-barked trees of stratum B, the calculated factor was ca. 7.

Of the 250 lichen species observed within the nine-tree subset, 219 occurred only from height

TABLE 2. Stratum A spatial distribution of lichen families on phorophytes, Suromoni, 1997–1998.

Families	Species per height zone					
	1	2	3	4	5	6
Arthoniaceae	1	3	3	5	2	3
Arthopyreniaceae	*			1	1	1
Bacidiaceae	3	3	5	6	2	
Coccocarpiaceae		2	3	6	7	3
Crocyniaceae				1	1	
Ectolechiaceae						1
Gomphillaceae					4	1
Graphidaceae	1	9	20	22	27	20
Gyalectaceae					1	1
incertis sedis					1	1
Lecideaceae s.l.	1					
Meruliaceae				1		
Opegraphaceae		1	1	1		
Parmeliaceae				2	4	3
Physciaceae					1	1
Pilocarpaceae	2	1	1	1		
Pyrenulaceae	2	2	2	3	3	1
Roccellaceae	1	6	6	6	4	
Solorinellaceae				1	1	
Thelotremataceae	7	19	22	19	13	9
Trichotheliaceae	1	2	1	1		
Trypetheliaceae	1	4	8	18	27	18
Verrucariaceae				1		
Total spp./ht. zone	20	52	72	95	99	63
Total families/ht. zone	10	11	11	17	16	13

* Blank cells = 0 spp. and thus 0 family representation in that height zone.

zone 2 upward. If only height zone 1 had been studied in the crane plot, 87% of total species richness would have been missed.

FIGURE 3 depicts vertical distribution patterns of recorded families growing on *Goupia glabra* and *Qualea* species in stratum A. Absolute numbers of different families per height zone show that the most diverse zones were in the inner canopy (17) and the middle canopy (16), followed by the outer canopy (13). The upper trunk and lower trunk had 11 families each, and lastly the trunk base had 10 families (TABLE 2). Within the three dominant families, Thelotremataceae, Graphidaceae, and Trypetheliaceae, a clear vertical stratification was obvious. Together with the less abundant Arthoniaceae and Pyrenulaceae, the three dominants were represented in each height zone and showed a remarkable reciprocal distribution. Thelotremataceae clearly dominated the ground level in species richness, with such families as Arthoniaceae, Graphidaceae, and Trypetheliaceae less well represented. Moving upward toward the first big ramifications, the proportion of the Graphidaceae and Trypetheliaceae increased continuously. The proportion of Thelotremataceae appeared to remain constant up to height zone 3, where this family reached its highest absolute species num-

ber. In height zone 4, the three dominants were more or less equally represented. Upward from height zone 4, Thelotremataceae became less important, and Graphidaceae and Trypetheliaceae were able to establish themselves. This pattern is congruent with the outline by Sipman and Harris (1989: 304). In the outer canopy, Graphidaceae and Trypetheliaceae supplied ca. 60% of overall species richness.

For the entire tree, three different distribution types can be recognized:

Lower forest layers. The first type, comprised of families that prefer the lower forest layers, faded out upwards. Trichotheliaceae, Melaspileaceae, Lecideaceae s.l., and Pilocarpaceae typically contributed to this type. Distribution patterns with a wider range were assigned, however, to Thelotremataceae, Bacidiaceae, and Pyrenulaceae.

Upper truck to middle canopy. Crocyniaceae, Gomphillaceae, Meruliaceae, and Solorinellaceae constituted the second type, with a high presence from the upper trunk to the middle canopy. Arthoniaceae and Roccellaceae also may be placed in this type.

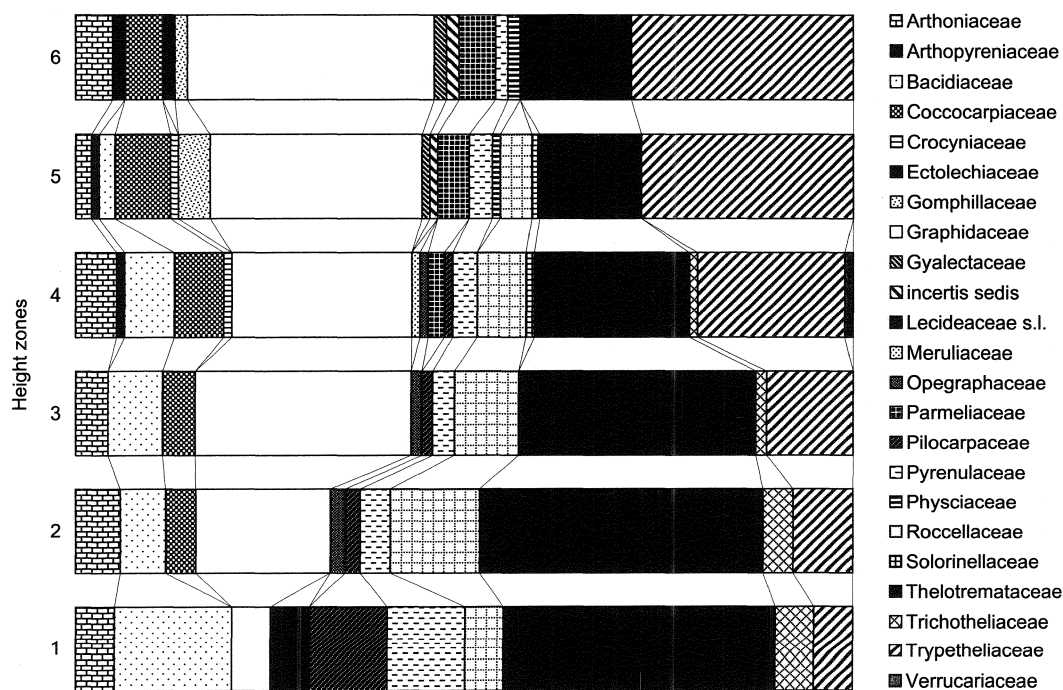**Upper canopy.** The third type is just the op-

FIGURE 3. Stratum A spatial distribution of lichen families on phorophytes (*Goupia glabra* and *Qualea* sp.) in percentage terms (for absolute values see TABLE 2).

posite of the first one. The large families Trypetheliaceae and Graphidaceae have a wider ecological range than the more narrowly distributed Arthopyreniaceae, Catillariaceae, Coccocarpiaceae, Gyalectaceae, Physciaceae, Parmeliaceae, and Ectolechiaceae.

The vertical distribution of families near Saül (Montfoort & Ek 1990), when compared with the proposed distribution types at Surumoni, appeared somewhat less pronounced. Near Saül, the Bacidiaceae, Lecideaceae s.l., and Trichotheliaceae, in agreement with the present study, were typical for the basal zones (first distribution type). The Thelotremataceae, however, were more or less equally dispersed across all strata, with a maximum in species richness in height zone 6. The rather light-demanding Coccocarpiaceae and Parmeliaceae (Cornelissen & ter Steege 1989: 144, Sipman & Harris 1989: 304), restricted to the higher zones at Surumoni, were observed even in the lowest height zone at Saül, suggesting better light conditions near the ground. No deviation was found, however, when comparing the distribution of the families Opegraphaceae and Roccellaceae, both characteristic of middle heights. At both sites, Graphidaceae and Trypetheliaceae were best represented in the outer canopy and faded out downwards.

For families on trees of stratum B at Suru-

moni, considering the low number (2) of sampled trees, an arrangement of species or families by elevational strata was preliminary and, at best, tendentious. Similar to the trees of stratum A, the predominating families were Thelotremataceae and Graphidaceae, while Trypetheliaceae lost out to Bacidiaceae. The 37 species of Thelotremataceae dominated aspects in all height zones except for the outer canopy, where Graphidaceae were more diverse. Trichotheliaceae and Bacidiaceae, which did not contribute to the upper canopy flora in stratum A, were found in the upper canopy of stratum B (TABLE 3).

With regard to internal beta diversity, a key criterion for spatial distribution patterns is species turnover along the vertical, environmental gradient within the forest stand, which indirectly reflects differences in ecological niches and represents the number of communities present (Wilson & Shmida 1984: 1056). Our study calculated beta turnover for all six adjacent height zones of the three *Goupia* individuals and for the four *Qualea* trees (FIGURE 4). While both curves are nearly parallel in the lower height zones, they approximate each other in the transition between height zones 5 and 6. The most striking feature is the high species turnover between height zones 1 and 2 for both phorophytes, which cor-

TABLE 3. Stratum B spatial distribution of lichen families on phorophytes, Suromoni, 1997–1998.

Families	Species per height zone					
	1	2	3	4	5	6
Arthoniaceae	2	2	1	1	2	1
Bacidiaceae	3	3	4	3	2	1
Coccocarpiaceae	*	1	1	2	2	1
Crocyniaceae		1				
Ectolechiaceae						1
Gomphillaceae					1	1
Graphidaceae	2	5	13	4	7	10
Gyalectaceae					1	1
Lecanoraceae	2	1	2			
Lecideaceae s.l.	1		1		1	
Melaspileaceae			1	1		
Opegraphaceae			1			
Pyrenulaceae	1	2	3	2	3	3
Roccellaceae			1			
Thelotremataceae	4	16	20	8	13	9
Trichotheliaceae		2	2	1	1	1
Trypetheliaceae			1	4	4	1
Total spp./ht. zone	15	33	51	26	37	30
Total families/ht. zone	8	10	14	10	12	12

* Blank cells = 0 spp. and thus 0 family representation in that height zone.

roborates the unique position of the tree base as well as the applied height zone system. Especially at the tree base, the rough and strongly weathered bark bears a peculiar lichen vegetation that differs considerably from the remaining trunk vegetation. The calculated beta turnover between height zones 1 and 2, however, may be little influenced by the smaller sample size in zone 1, even though the index is standardized by sample richness. For *Goupia glabra,* species replacement is generally lower in height zones

FIGURE 4. Average beta turnover values (β_T), according to Wilson and Shmida (1984), of adjacent height zones for *Goupia glabra* and *Qualea* sp. (both stratum A).

1 to 5 as a result of the overriding effect of the unstable bark condition. The small bark ridges are ephemeral and can be colonized only by a set of specially adapted lichens. This synusia, which does not vary greatly over the entire trunk, leads to relatively low beta turnovers ($\beta_T = 0.5$). Higher up, when the substratum becomes similar to that of *Qualea,* species turnover gradually increases. *Qualea* itself reveals a nearly entire species exchange between height zones 1 and 2 ($\beta_T = 0.95$); β_T then remains constant at ca. 0.7, until it drops slightly between height zones 5 and 6.

The additive beta diversity of all height zones, taking into account the cited restrictions, roughly reflects the degree of total species turnover. The additive beta diversity, averaged for all *Qualea* trees, is 3.5 or more than three complete turnovers in species composition from tree base to twigs. Beta diversity for all height zones of *Goupia glabra* is as low as 2.7, which again demonstrates the considerable influence of substratum on lichen colonization.

In FIGURE 5, species turnover is plotted as the average between the height zones of all trees of stratum A and stratum B respectively. Even though stratum B is represented by only two phorophytes, its main difference from rough-barked trees of stratum A apparently is a comparatively small species turnover in the transition between tree base and lower trunk. One explanation may be the more uniform substratal conditions over the entire bole on the smaller
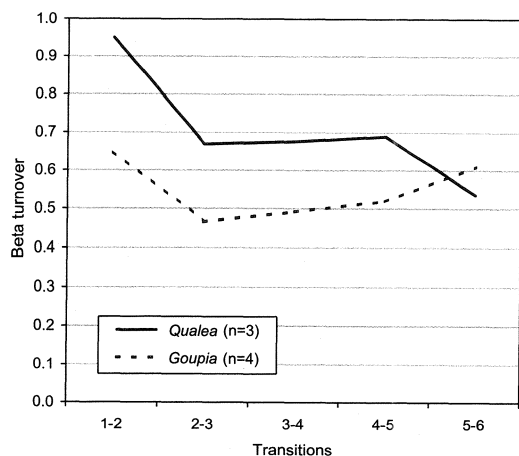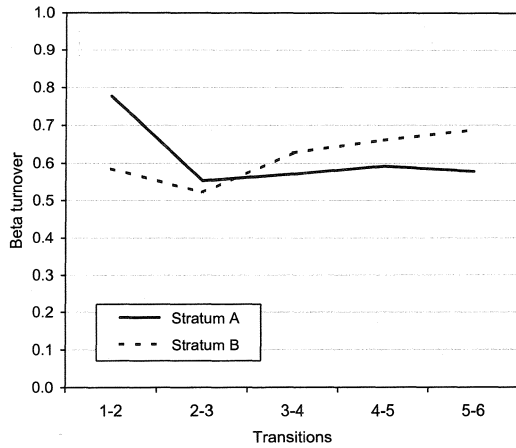
FIGURE 5. Average beta turnover values (β_T), according to Wilson and Shmida (1984), of adjacent height zones for trees of strata A and B, respectively.

stratum B trees, which provides a less differentiated habitat.

Change in the lichen species spectrum along the vertical gradient also is depicted in FIGURE 6, where species similarity is calculated, not only for adjacent height zones, but also for separated ones. As expected, species similarity declines gradually if, for example, the tree base is compared with the zones above. The same applies if zone 2 is compared with zones 3 to 6 and so on. An example is given for trees of stratum A, where height zones 1 and 2 show a species similarity of 23%; height zones 1 and 3, still 14%; height zones 1 and 4, only 9%; height zones 1 and 5, about 4%; and height zones 1 and 6 do not share even one species (0%). In comparing species similarities between height zones among forest strata A and B, a clear distinction is obvious. Typically, trees of stratum B have less pronounced differences in species composition between tree base and canopy, which can be explained by the paucity of discriminative microhabitats (uniform bark structure) combined with less distinct climatic gradients. To show this effect for both forest strata and all height zones in one diagram, Sørensen indices of neighboring height zones (separated by one zone in between and so on) are averaged over all phorophytes in a stratum (FIGURE 7). Although average similarities for neighboring height zones are nearly equal for trees in both strata, they differ more and more when comparing increasingly separated height zones.

CONCLUSIONS

A comparison of our study results with available data in the cited literature reveals that tropical lowland rain forests are not necessarily as
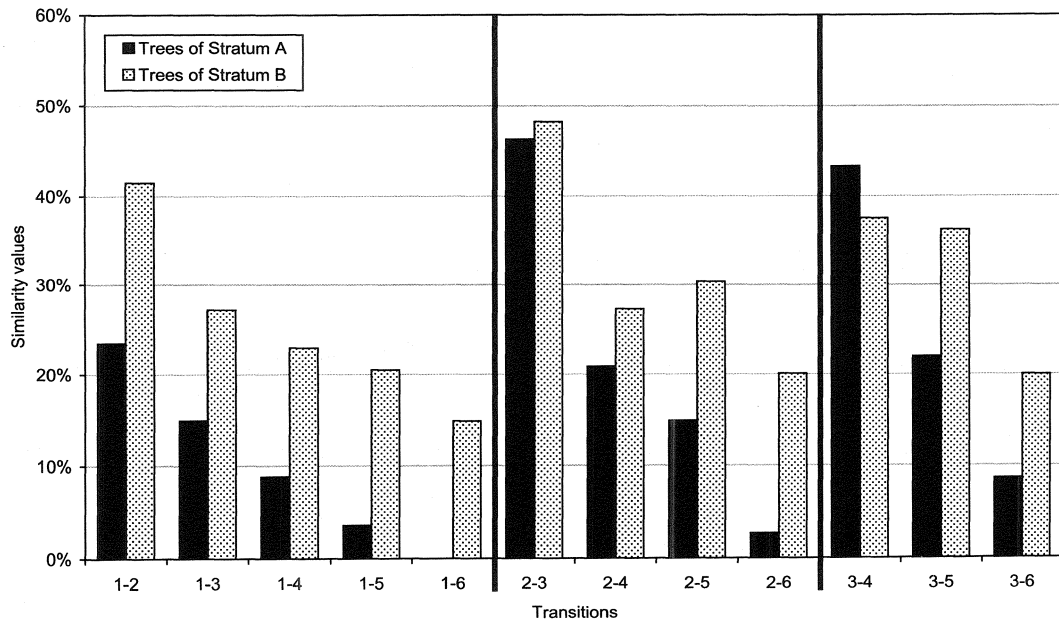

FIGURE 6. Mean values of indices according to Sørensen (1948) comparing, respectively, the lichen composition of height zone 1 with all other height zones, and those of height zones 2 and 3 with all higher height zones.
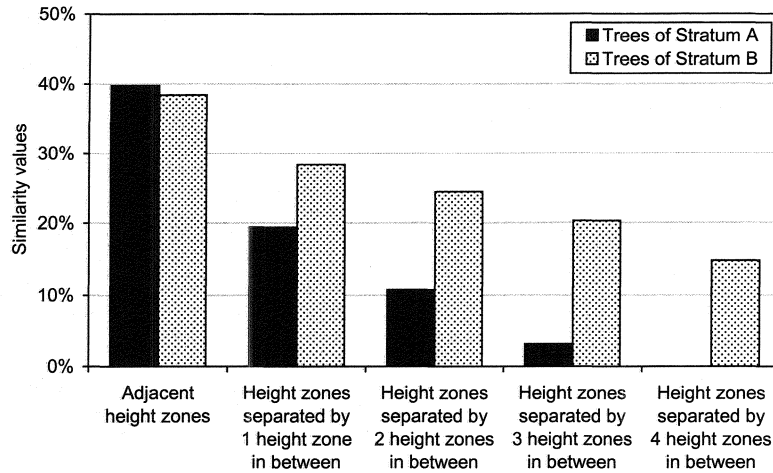
FIGURE 7.   Mean values of indices according to Sørensen (1948) between neighboring height zones, height zones separated by one zone in between, height zones separated by two zones in between, and so on.

poor in lichenized fungi as previously thought. About 70% of total species richness in the investigated Amazon lowland rain forest is contributed by three crustose families of lichenized fungi: Thelotremataceae, Graphidaceae, and Trypetheliaceae.

In lowland rain forests, a remarkable percentage of lichen species diversity is hidden in the upper forest regions, out of reach for unequipped scientists. If studies are limited to bark epiphytes of height zone 1, then 80–90% of the effective species diversity is overlooked.

For rough-barked trees of stratum A, species turnover along the vertical scale is highest between tree base and lower trunk, a pattern not found for trees of stratum B.

Based on the high beta diversity calculated for canopy trees over all height zones, a complete species turnover can be said to occur three to four times from tree base to twigs.

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LITERATURE CITED

Aptroot, A. 1997a. Lichen biodiversity in Papua New Guinea, with the report of 173 species on one tree. Pp. 203–213 *in* R. Türk and R. Zorer, eds. Progress and Problems in Lichenology in the Nineties-IAL3. Biblioth. Lichenol. 68. Cramer, Berlin.

———. 1997b. Species diversity in tropical rainforest ascomycetes: lichenized versus non-lichenized; foliicolous versus corticolous. Növenyrendsz. Növényföldr. Tranz., Eötvös Loránd Tudományegyet. Budapest 21(1): 37–44.

Aptroot, A. and H.J.M. Sipman 1997. Diversity of lichenized fungi in the tropics. Pp. 93–106 *in* K.D. Hyde, ed. Biodiversity of Tropical Microfungi. University Press, Hong Kong.

Aptroot, A., P. Diederich, E. Sérusiaux and H.J.M. Sipman. 1995. Lichens and lichenicolous fungi of Laing Island (Papua New Guinea). Pp. 19–48 *in* J.G. Knoph, K. Schrüfer and H.J.M. Sipman, eds. Studies in Lichenology with Emphasis on Chemotaxonomy, Geography and Phytochemistry. Festschrift Leuckert. Biblioth. Lichenol. 57. Cramer, Berlin.

———. 1997. Lichens and lichenicolous fungi from New Guinea. Biblioth. Lichenol. 64: 1–220.

Coomes, D.A. and P.J. Grubb 1996. Amazonian caatinga and related communities at La Esmeralda, Venezuela: forest structure, physiognomy and floristics, and control by soil factors. Vegetatio 122: 167–191.

Cornelissen, J.H.C. and S.R. Gradstein. 1990. On the occurrence of bryophytes and macrolichens in dif-

ferent lowland rain forest types at Mabura Hill, Guyana. Trop. Bryol. 3: 29–35.

Cornelissen, J.H.C. and H. ter Steege 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. J. Trop. Ecol. 5: 131–150.

Feige, G.B., H.T. Lumbsch, S. Huneck and J.A. Elix 1993. Identification of lichen substances by a standardized high-performance liquid chromatographic method. J. Chromatogr. 646: 417–427.

Gradstein, S.R. 1995. Biodiversity of non-vascular epiphytes in tropical forests. Pp. 34–36 in R. Lücking, M. Freiberg, A. Lücking, E. Freiberg and G. Gottsberger, eds. Second International ESF-Workshop on Tropical Canopy Research. Final Scientific Report. Ulm.

Gradstein, S.R. and T. Pócs. 1989. Bryophytes. Pp. 311–325 in H. Lieth and M.J.A. Werger, eds. Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies. Elsevier, Amsterdam.

Hale, M.E. 1974. Morden-Smithsonian Expedition to Dominica: The Lichens (Thelotremataceae). Smithsonian Contr. Bot. 16: 1–45.

———. 1978. A revision of the lichen family Thelotremataceae in Panama. Smithsonian Contr. Bot. 16: 1–58.

Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr. Suec. 59: 1–129.

Kira, T. and K. Yoda 1989. Vertical stratification in microclimate. Pp. 55–71 in H. Lieth and M.J.A. Werger, eds. Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies. Elsevier, Amsterdam.

Komposch, H. and J. Hafellner. 1999. List of lichenized fungi so far observed in the tropical lowland rain forest plot Surumoni (Venezuela, Estado Amazonas). Fritschiana 19: 1–10.

Longman, K.A. and J. Jeník. 1987. Tropical forest and its environment. 2nd Edition, Longman Scientific & Technical, Harlow.

Lücking, R. "Foliikole Flechten und ihre Mikrohabitatpräferenzen in einem tropischen Regenwald in Costa Rica." Ph.D. diss., University of Ulm, Germany, 1994.

———. 1995. Foliikole Flechten auf Cecropiaceen im Kronendach eines tropischen Regenwaldes. Pp. 261–274 in E.E. Farkas, R. Lücking and V. Wirth, eds. Scripta Lichenologica–Lichenological Papers Dedicated to Antonin Vezda. Biblioth. Lichenol. 58. Cramer, Berlin.

———. 1997a. Estado actual de las investigaciones sobre líquenes folíicolas en la region Neotropica, con un análisis biogeográfico preliminár. Trop. Bryol. 13: 87–114.

———. 1997b. The use of foliicolous lichens as bioindicators in the tropics, with special reference to the microclimate. Növenyrendsz. Növényföldr. Tranz., Eötvös Loránd Tudományegyet. Budapest 21(1): 99–116.

———. 1998a. Foliicolous lichens and their lichenicolous fungi collected during the Smithsonian International Cryptogamic Expedition to Guyana 1996. Trop. Bryol. 15: 45–76.

———. 1998b. Ecology of foliicolous lichens at the 'Botarrama' trail (Costa Rica), a neotropical rain forest. III. Phorophyte ranges and patterns of phorophyte preferences. Phyton (Horn) 38: 195–219.

Lücking, R. and M. Matzer. 1996. Ergänzungen und Verbesserungen der foliikolen Flechtenflora Costa Ricas. Die Familie Opegraphaceae (einschließlich der Gattung Mazosia). Nova Hedwigia 63: 109–144.

Montfoort, D. and R.C. Ek. "Vertical Distribution and Ecology of Epiphytic Bryophytes and Lichens in a Lowland Rain Forest in French Guiana." Masters thesis, Utrecht University, Utrecht, Netherlands, 1990.

Peet, R.K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5: 285–307.

Perry, D.R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10(2): 155–157.

Rhoades, F.M. 1995. Nonvascular epiphytes in forest canopies: distribution, abundance, and ecological roles. Pp. 353–408 in M.D. Lowman and N.M. Nadkarni, eds. Forest Canopies. Academic Press, San Diego.

Richards, P.W. 1984. The ecology of tropical forest bryophytes. Pp. 1233–1270 in R.M. Schuster, ed. New Manual of Bryology, Vol. 2., Nichinan, Miyazaki, Japan.

———. 1996. The Tropical Rain Forest: An Ecological Study. 2nd Edition, University Press, Cambridge.

Shannon, C.E. 1949. The mathematical theory of communication. Pp. 29–125 in C.E. Shannon and W. Weaver, eds. The Mathematical Theory of Communication. University of Illinois Press, Urbana. 1963 ed., Illini Books, Chicago.

Sipman, H.J.M. 1989. Lichen zonation in the parque Los Nevados transect. Stud. Trop. Andean Ecosystems 3: 461–483.

———. 1992. Results of a lichenological and bryological exploration of Cerro Guaiquinima (Guayana Highland, Venezuela). Trop. Bryol. 6: 1–31.

———. 1997a. Additions to the lichen flora of Araracuara (Colombian Amazonia). Caldasia 19(1–2): 247–255.

———. 1997b. Observations on the foliicolous lichen and bryophyte flora in the canopy of a semi-deciduous tropical forest. Növenyrendsz. Növényföldr. Tranz., Eötvös Loránd Tudományegyet. Budapest 21(1): 153–161.

Sipman, H.J.M. and A. Aptroot. 1992. Results of a botanical expedition to Mount Roraima, Guyana. II. Lichens. Trop. Bryol. 5: 79–107.

Sipman, H.J.M. and R.C. Harris. 1989. Lichens. Pp. 303–309 in H. Lieth and M.J.A. Werger, eds. Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies. Elsevier, Amsterdam.

Sipman, H.J.M. and R.J.M.T. van Aubel. 1992. New Parmeliaceae (lichenes) from the Guianas and surroundings. Mycotaxon 44(1): 1–12.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to

analyses of the vegetation on Danish commons. Biol. Skr. 5(4): 1–34.

White, F.J. and P.W. James. 1985. A new guide to microchemical techniques for the identification of lichen substances. Bull. Brit. Lichen Soc. 57(Suppl.): 1–45.

Whittaker, R.H. 1977. Evolution of species diversity in land communities. Pp. 1–67 *in* M.K. Hecht, W.C. Steere and B. Wallace, eds. Evolutionary Biology. Plenum Press, New York.

Wilson, M.V. and A. Shmida. 1984. Measuring beta diversity with presence-absence data. J. Ecol. 72: 1055–1064.

Wolf, J.H.D. 1993a. Epiphyte communities of tropical montane rain forests in the northern Andes. I. Lower montane communities. Phytocoenologia 22(1): 1–52.

———. 1993b. Epiphyte communities of tropical montane rain forests in the northern Andes. II. Upper montane communities. Phytocoenologia 22(1): 53–103.

———. 1993c. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. Ann. Missouri Bot. Gard. 80: 928–960.